

Zanclea* species (Hydroidomedusae, Anthomedusae) from the Mediterranean

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SUMMARY: Three species of hydroids referable to the genus *Zanclea* are recorded from the Apulian waters (Ionian Sea). Species distinction is based mainly on cnidome, and especially on the morphology and position of macrobasic euryteles: *Zanclea sessilis* growing on bryozoans, with apotrichous macrobasic euryteles with shaft coiled in a horseshoe shape, disposed in a circle around the hypostome, and in the hydrorhiza; *Zanclea costata* growing on bivalve shells, with holotrichous (?) macrobasic euryteles with a spirally coiled shaft, abundant in the hydrorhiza and rare in the hydranth body; and *Zanclea* sp. growing on bryozoans, with apotrichous macrobasic euryteles of two sizes, both with shaft coiled along the long axis of the capsule, dispersed in the hydranth body and in the hydrorhiza. The hydroids of *Zanclea sessilis* and *Zanclea* sp. were reared under identical controlled conditions for more than one year, but their morphological features remained unchanged and they both produced medusae. The medusae of *Zanclea sessilis* were reared to maturity, those of *Zanclea* sp. just to a young age. The main difference between the medusae was the consistent presence of an enlargement of the middle part of radial canals in *Zanclea sessilis* (from newly released to adult specimens), a feature lacking in *Zanclea* sp. It is confirmed that, as already suggested by several authors, cnidome is a reliable feature for species identification of *Zanclea* hydroids, but medusa identification remains more problematic. In spite of the widespread claim that *Zanclea* is represented world-wide by a single species, it is here demonstrated that the genus comprises at least three species in the Mediterranean.

Key words: *Zanclea*, Hydromedusae, taxonomy, life cycle, nematocysts, Mediterranean sea.

INTRODUCTION

The taxonomy of *Zanclea* hydroids and medusae, as remarked by Petersen (1990), is in "a state of chaos" (see Bouillon, 1985; Petersen, 1990; and Boero *et al.*, 1995, for definition of the genus *Zanclea* and of the family Zancleidae). The genus name *Zanclea* was itself in jeopardy, as a junior synonym, until conserved as a zoological name (International Commission On Zoological Nomenclature, 1994) following a case raised by Calder (1992). The medusae of *Zanclea* are characterized by tentacular cnidophores containing macrobasic

euryteles and by exumbrellar pouches containing stenoteles. The hydroids have many capitate tentacles scattered or in irregular verticils on the hydranth body and usually have stenoteles and macrobasic euryteles (but these are absent in some species). *Zanclea* hydroids have been reported growing on algae or rocks but they are more often symbiotic with other animals, namely: bryozoans, bivalve molluscs, corals, gorgonians, compound ascidians, and barnacles.

Russell and Rees (1936) attempted a revision of the genus and, as a result of both rearing experiments and literature data, considered *Zanclea implexa* (Alder, 1857) identical with *Z. gemmosa* McCrady, 1859, and retained it as possibly distinct from *Z. costata* Gegenbaur, 1856 from the

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Mediterranean, this having four marginal tentacles in the adult medusa instead of two. Russell (1953) considered *Z. costata* as identical with *Z. implexa*, hypothesising that all described *Zanclea* species could be referable to *Z. costata*. Russell did not consider the cnidome as a taxonomic feature in species of the genus. The cnidome had been utilised by Hastings (1930) who distinguished the hydroid *Z. protecta* Hastings, 1930 from other *Zanclea* species due to the absence of macrobasic euryteles. Hastings, a bryozoan specialist, was actually the first to base a new *Zanclea* species on cnidome features. Weill (1934) described the cnidome of several *Zanclea* species. Kramp (1961) recognized three medusa-based species of *Zanclea*, namely: *Z. costata*, *Z. dubia* Kramp, 1959, and *Z. orientalis* Browne, 1916. Picard (1965) reported two *Zanclea* hydroids from the Mediterranean Sea: *Z. costata* living on bivalve molluscs and having holotrichous macrobasic euryteles with a spirally coiled shaft in the undischarged capsule, and *Z. sessilis* (Gosse, 1853) living on bryozoans and having apotrichous macrobasic euryteles with a horseshoe coiled shaft in the undischarged capsule. This was further supported by Berhaut (1969) who, studying plankton samples, reported the medusae of *Z. costata* as having four tentacles at maturity, whereas those of *Z. sessilis* had two, a distinction, however, not based on actual observation of the formation of new tentacles under controlled conditions. Rees and Roa (1966) reported on a medusa with polyps growing from the manubrium and bearing medusa buds, and identified their material as *Z. implexa*. Cnidome-based distinction of the hydroid stage was accepted by Millard and Bouillon (1973) who refrained from identifying some of their *Zanclea* material due to lack of information on both cnidome and life cycle.

Bouillon (1974), reviewed the available knowledge on the cnidome of the Zancleidae, reporting on five recognized species: *Z. costata*, *Z. sessilis*, *Z. indica* Mammen, 1963, *Z. dubia*, and *Z. orientalis*. Uchida and Sugiura (1976) described a new species of *Zanclea* from medusae producing medusa buds: *Z. prolifera* Uchida and Sugiura, 1976. This species was reported as valid by Bouillon (1978) who, however, was cautious in identifying *Zanclea* medusae from Papua New Guinea at species level. Hirohito (1988), due to the presence of ocelli, referred *Z. prolifera* to *Teissiera*. Brinckmann-Voss (1970) disregarded Picard's distinction of *Zanclea* species based on cnidome and concurred with

Russell (1953) in recognizing just one species, together with the subspecies *Z. costata* var. *neapolitana* Brückner, 1914 which lived on bivalve shells. Hirohito (1988) found *Zanclea* hydroids associated with bryozoans and algae but refrained from naming them, implying disbelief that *Zanclea* comprised a single species. Calder (1988), on the contrary, agreed with Brinckmann-Voss (1970) and considered *Zanclea* as comprising a single species: invoking the law of priority, he referred all nominal *Zanclea* species to *Z. alba* (Meyen, 1834), a species found growing on algae and lacking the macrobasic euryteles typical of other *Zanclea* species. He later (Calder, 1992) acknowledged that taxonomic questions remained regarding the status of various nominal species of *Zanclea*, including *Z. alba*, *Z. sessilis*, *Z. implexa*, and *Z. costata*.

According to Picard's (1965) treatment of Mediterranean *Zanclea*, the species that Brinckmann-Voss (1970) regarded as *Z. costata* should be *Z. sessilis*, whereas *Z. costata* var. *neapolitana* should be *Z. costata*.

Such distinctions, however, stem from insufficient diagnostic features in the original descriptions of both *Z. sessilis* and *Z. costata*, and of all other nominal species assigned to the genus. The criterion of using hydroid cnidome (in terms of nematocyst types) and structural differences within the same nematocyst type as the most reliable characters on which to base species distinction is possibly a starting point to disentangle the chaos in *Zanclea* taxonomy. Medusan features are, at present, less diagnostic than hydroid ones, since cnidomes seem rather uniform and a feature like tentacle number (two or four) was reported as changing with age by Goy (1972). In tropical seas, with constantly high temperatures, *Zanclea* medusae invariably have two tentacles (Bouillon, 1978), whereas at temperate latitudes tentacle number can be four. Due to the tropic-like features of the Mediterranean in the summer, and to its temperate features in the winter (Boero and Bouillon, 1993), this sea might host different cohorts of the same species, with differing features according to water temperature. Varying environmental conditions, however, have never been shown to account for differences in cnidome. Possibly, nematocyst size is not a reliable taxonomic character, since Vannucci (1960), by rearing experiments, reported on variation in nematocyst size for both hydroids and medusae of *Merga tergestina* (Neppi and Stiasny, 1913), but no cnidome variation was ever reported.

The treatment of the Mediterranean *Zanclea* species by Picard (1965) was, and still is, widely overlooked for several reasons, possibly linked to his over-synthetic phrasing and to the absence of illustration. Millard and Bouillon (1973) and Bouillon (1974), however, followed Picard (1965) and re-stated the distinctive features of the two Mediterranean *Zanclea* species.

Availability of new material from the coasts of Apulia, Southern Italy, provided an opportunity to

test the validity of two differing approaches to the taxonomy of *Zanclea*: a lumping one, disregarding cnidome features and considering just one species as valid, and a splitting one, giving cnidome a great taxonomic weight and envisaging *Zanclea* as a speciose genus.

MATERIALS AND METHODS

Hydroid colonies were collected along the Ionian coast of Apulia:

– A sterile colony, later identified as *Zanclea costata* on July 1991, growing on a shell of *Cardium* sp.;

– A sterile colony of *Zanclea sessilis* on March 1993, on a bryozoan (*Beania* sp.);

– A sterile colony, later identified as *Zanclea* sp. on June, 1993, on another, unidentified, bryozoan.

The hydroid of *Z. costata* was preserved immediately after collection, whereas polyps of the colonies of *Z. sessilis* and *Z. sp.* were explanted on microscope slides and cultured in aerated vessels of 2 l, kept in a thermostatic chamber. Temperature and photoperiod were regulated to match field variations. Sea-water, filtered through a 0.45 µm mesh, was changed every two-three days, after providing *Artemia* nauplii for food.

Colonies were examined daily to detect incipient medusa buds. When these started to develop, the microscope slides were transferred into small cups with no aeration. Water was changed daily, after the feeding session. Liberated medusae were transferred into other vessels and kept under the same environmental conditions as the hydroids.

RESULTS

Zanclea sessilis (Gosse, 1853) (Figs 1, 2)

Hydroid

Colony stolonal, hydrorhiza covered by the bryozoan skeleton (see Material) in the central part of the colony and uncovered at its margin. Hydranths with 4-6 oral capitate tentacles and 20-40 aboral capitate tentacles, scattered on the distal 3/4 of hydranth column. Hypostome milk-white, column transparent, with reddish gastric walls. Perisarc thin, encrusted by sediment particles, not annulated, whitish. Medusa buds growing below the tentacled part

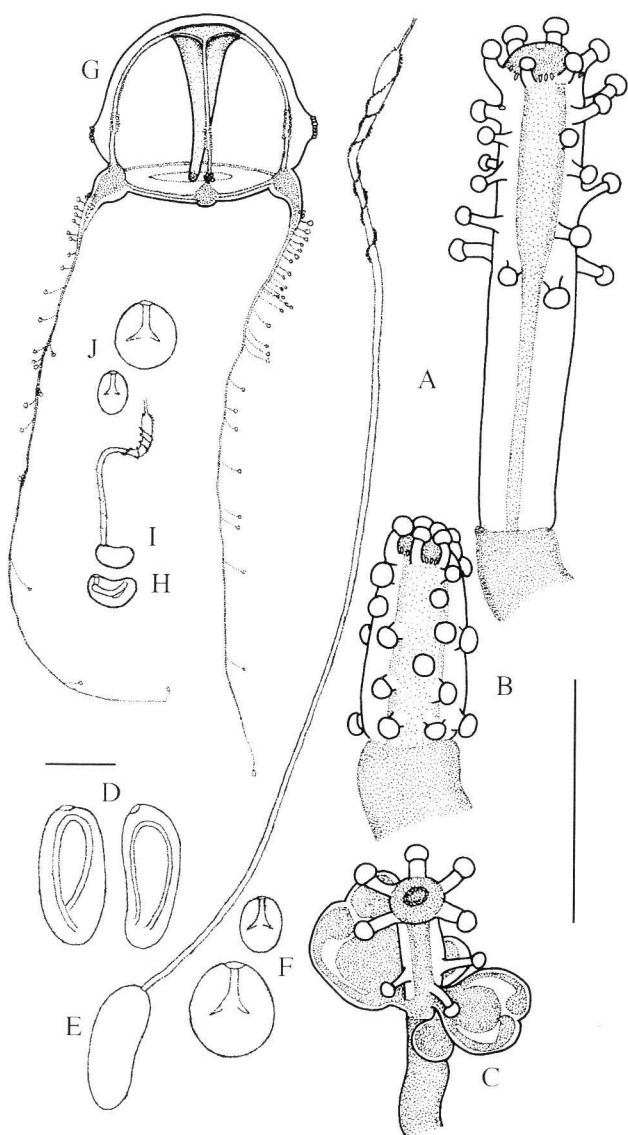


FIG. 1. – *Zanclea sessilis*. A: extended, living hydranth; B: the same, contracted; C: reduced living hydranth, bearing medusa buds; D: hydroid, undischarged macrobasic euryteles in "frontal" and "lateral" view; E: the same, discharged; F: hydroid, undischarged stenoteles of two sizes; G: newly released medusa with stretched manubrium; H: medusa, undischarged macrobasic eurytele; I: the same, discharged; J: medusa, undischarged stenoteles of two sizes. Bar scales: A, B, C: 1 mm; all nematocysts: 0.01 mm; diameter of medusa 0.4 mm.

of hydranth, fertile hydranths gradually reducing in size and tentacle number.

Nematocysts:

- stenoteles of two sizes in tentacle capitations;
- apotrichous macrobasic euryteles with shaft coiled in a horseshoe shape, covered with spines for one fifth of its length when extruded, disposed in a circle in between oral tentacles and in hydrorhiza, rare in the hydranth column.

Colonies kept in the laboratory under controlled temperature conditions produced medusae from mid-September (24 °C) to the first week of October, 1993 (23 °C). From mid-April 1994, in order to have more medusae, the colonies were kept at a constant temperature of 24 °C, but produced medusae only from May 25th to June 1st.

Medusa

Newly released

Bell almost spherical, 0.3-0.4 mm in diameter, with an almost quadrate margin. Four radial canals, each with a median thickening having a structure similar to that of tentacular bulbs. Manubrium quadrate at base, reaching more than half of subumbrellar cavity. Mouth round, armed with stenoteles. Four exumbrellar nematocyst pouches, each containing 8-12 stenoteles, immediately above tentacular bulbs, narrow at base and widening distally, extending for one fifth of exumbrella. Gonads absent. Two perradial tentacular bulbs, triangular, bearing one long tentacle each, and two smaller perradial tentacular bulbs, triangular, deprived of tentacles. Tentacles three times as long as exumbrella when fully extended, bearing cnidophores (with 2-3 nematocysts each) on their external margin.

Nematocysts of two types:

- apotrichous macrobasic euryteles in cnidophores;
- stenoteles of two sizes around the mouth and in exumbrellar pouches.

Adult

One-month-old medusa 1 mm high, bell shaped, with two well developed perradial tentacles. Bell greenish. Sperm masses developing in four interradial areas of manubrium. Four radial canals, each with a median thickening having a structure similar to that of tentacular bulbs. Manubrium almost reaching velar opening. Exumbrellar nematocyst pou-

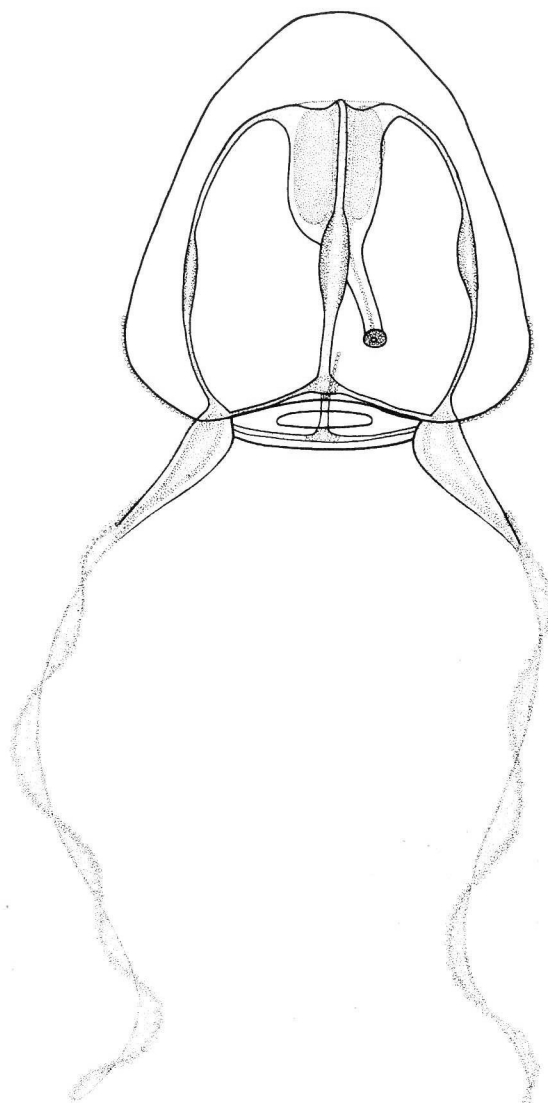


FIG. 2. – *Zanclea sessilis*. Mature, laboratory reared, one-month-old medusa. Bell height 1 mm.

ches linear and narrow, extending for one fourth of exumbrella. Two tentacled tentacular bulbs, triangular and long, with tentacles 12-13 times as long as exumbrella, ribbon like due to hundreds of cnidophores on their external margin. Two small atentaculate tentacular bulbs.

Behaviour

Medusae were fed individually by hand. Only on rare occasions were *Artemia* nauplii caught by the tentacles, which contracted together with the umbrella so that nauplii were passed to the mouth. Tentacle pieces were regularly found on the bottom of the rearing jars.

Remarks

Zanclea sessilis was originally described by Gosse (1853) from the coast of England as *Coryne sessilis*. The original description and figures are rather general and no types are available, so it is unclear whether the Mediterranean material (or even the British one) can be referred to this nominal species. For sake of stability, however, it seems unwise yet to propose a new name for the Mediterranean form, pending detailed studies of British material. Hincks (1868) described colonies of *Z. implexa*, considered as identical with *Z. sessilis*, growing on the bryozoan *Cellepora*. Picard (1965) recorded it from the Mediterranean as being smaller than *Z. costata*. In the Mediterranean Sea, Berhaut (1969) reported the adult medusa of *Z. sessilis* as having two tentacles and being smaller than the adult, four-tentacled medusa of *Z. costata*. Goy (1972) reported *Zanclea* medusae with medially thickened radial canals as being juveniles, but she also reported mature medusae with such character. Our results demonstrate that the radial canals remain locally thickened for the whole life of the medusa, and that maturity is reached without increase in tentacle number. The present material agrees with both hydroid and medusa described as *Zanclea costata* by Brinckmann-Voss (1970). Macrobasic euryteles with shaft coiled in a horseshoe shape were found in specimens labelled *Zanclea costata*, deposited by A. Brinckmann, both at the Natural History Museum, London (BMNH 1974.11.21.38) and at the Stazione Zoologica di Napoli. Material deposited by Russell and Rees at the Natural History Museum, London, and labelled *Zanclea implexa* (BMNH, 1985.9.1.18; BMNH 1970.1.9.1) had macrobasic euryteles with shafts coiled as in the preceding specimens, and is currently identified as *Zanclea sessilis*.

Zanclea costata Gegenbaur, 1856 (Fig. 3)

Hydroid

Colony of few polyps growing on margin of bivalve shell. Hydrocaulus covered by corrugated perisarc, not expanded at hydranth base. Preserved hydranths cylindrical, with about 60 capitate aboral tentacles scattered over all hydranth body, and an oral whorl of 4-5 tentacles. Small medusa buds between tentacles in mid-low part of hydranth.

Nematocysts:

- stenoteles of two sizes in tentacle capitations;

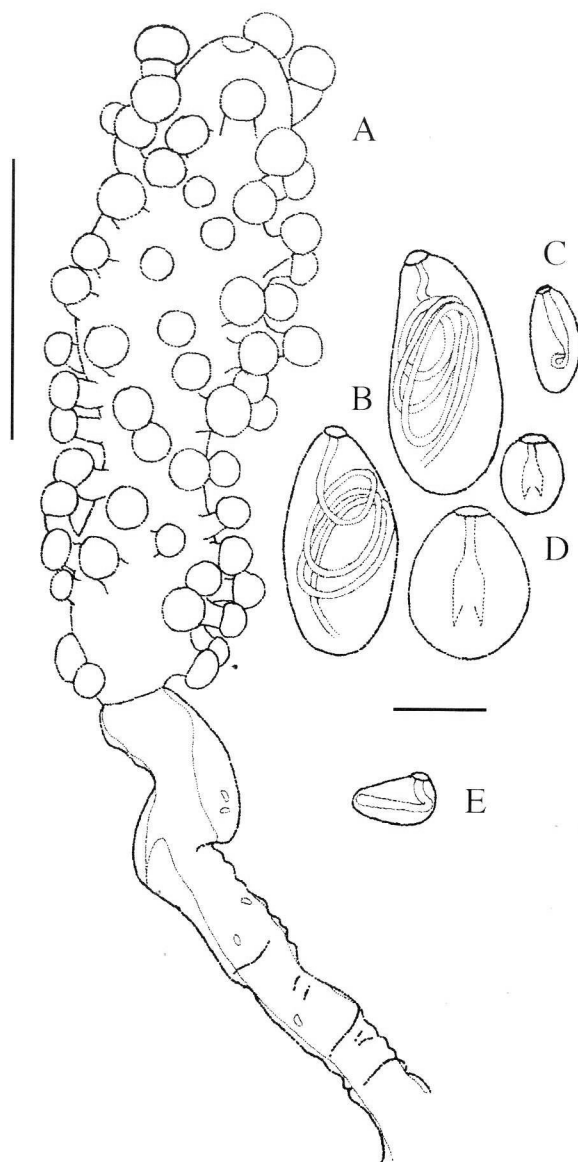


Fig. 3. – *Zanclea costata*. A: preserved hydranth; B: undischarged macrobasic euryteles in "frontal" and "lateral" view; C: undischarged microbasic eurytele (?); D: stenoteles of two sizes; E: macrobasic euryteles found in the hydranth budding zone. Bar scales: A: 1 mm; all nematocysts: 0.01 mm.

– macrobasic euryteles with a spirally coiled shaft in undischarged capsules, abundant in hydrorhiza and rare in hydranth body;

– microbasic euryteles (?), rare in tentacle capitations.

Remarks

Due to its small size the colony was immediately fixed after collection, so the above description is based on preserved material. Presumably, the

living hydranths are much longer than the figured one. Discharged nematocysts were not seen, but the slight shade visible throughout the coiled shaft suggests that the macrobasic euryteles are holotrichous. In undischarged macrobasic euryteles, in fact, it is the "armed" part of the shaft that can clearly be seen within the capsule, so that in *Z. sessilis* and *Z. sp.* the apotrichous shafts have a short marked part, the rest being without marking, whereas in *Z. costata* the shaft is clearly distinguishable for its whole length, being so recognizable as holotrichous. Both substrate and cnidome are in accordance with the description by Picard (1965), even though the rare microbasic eurytele is a further character not previously reported. The nematocysts in the medusa buds were the typical macrobasic euryteles of *Zanclea* medusae. This material resembles the *Z. costata* var. *neapolitana* described by Brinckmann-Voss (1970). Macrobasic euryteles with spirally coiled shaft were found in specimens labelled *Zanclea costata* var. *neapolitana*, deposited by A. Brinckmann both at the Natural History Museum, London, (BMNH 1974.11.21.39) and at the Stazione Zoologica di Napoli.

Zanclea sp. (Fig. 4)

Hydroid

Colony stolonal, hydrorhiza covered by the bryozoan skeleton in the central part of the colony and uncovered towards the margin. Hydranths with a whorl of 4 to 8 oral capitate tentacles and 50-60 aboral capitate tentacles scattered over the whole hydranth body. Hypostome whitish, hydranth transparent with pink-salmon gastric walls. Perisarc brownish and slightly wrinkled. Medusa buds growing among tentacles in the lower third of hydranth.

Nematocysts:

- stenoteles of two sizes in tentacle capitations.
- apotrichous macrobasic euryteles of two sizes, both with shaft coiled along the long axis of capsule, the bigger one with spines for one fifth of its length when extruded, the smaller one with spines for one tenth of its length, both present in hydrorhiza and in hydranth body;

Colonies kept at 24 °C produced medusae in the second half of August 1993. From mid-April 1994, in order to have more medusae, the colonies were kept at 24 °C, but they produced medusae only July 9-13th.

Newly released Medusa

Bell almost spherical, 0.4-0.5 mm in diameter, with an almost quadratic margin. Four radial canals with no median thickening. Manubrium quadratic at base, reaching half of subumbrellar cavity. Mouth round, armed with stenoteles. Four round exumbrellar nematocyst pouches, right above tentacular bulbs. Gonads absent. Two perradial tentacular bulbs, triangular, bearing one long tentacle each, and two smaller perradial tentacular bulbs, triangular, deprived of tentacles. Tentacles three times as long as bell when fully extended, bearing cnidophores (with 2-3 nematocysts each) on their outer side.

Nematocysts:

- stenoteles of two sizes around the mouth and in exumbrellar pouches.
- microbasic euryteles (?) rare on exumbrella (not observed as discharged) and absent from two-day old medusae;
- apotrichous macrobasic euryteles in cnidophores;

Behaviour

The medusae were fed with *Artemia* nauplii but feeding failed after a few days and they could not take food even when offered by hand. Also, homogenised *Mytilus* hepatopaneas was refused. The medusae died of starvation without reaching maturity.

Remarks

The hydroid showed a high morphological plasticity, with stolonisation, and hydranth formation from the area of medusa-bud production. These phenomena were more marked at 23-25 °C. The general morphology recalled *Zanclea costata*, but the nematocysts were much different, as was the host (a bryozoan instead of a bivalve). The macrobasic euryteles of two types were quite a distinctive character and it is probable that this will prove to be an undescribed species. Since many nominal species of *Zanclea* have been based on adult medusae, it is also possible that the adult medusa will be referable to one of those. The radial canals were not medially thickened in any of the observed new-born medusae, so this feature should not be considered as typical of juveniles, as suggested by Goy (1972), but is a specific character of *Zanclea sessilis*.

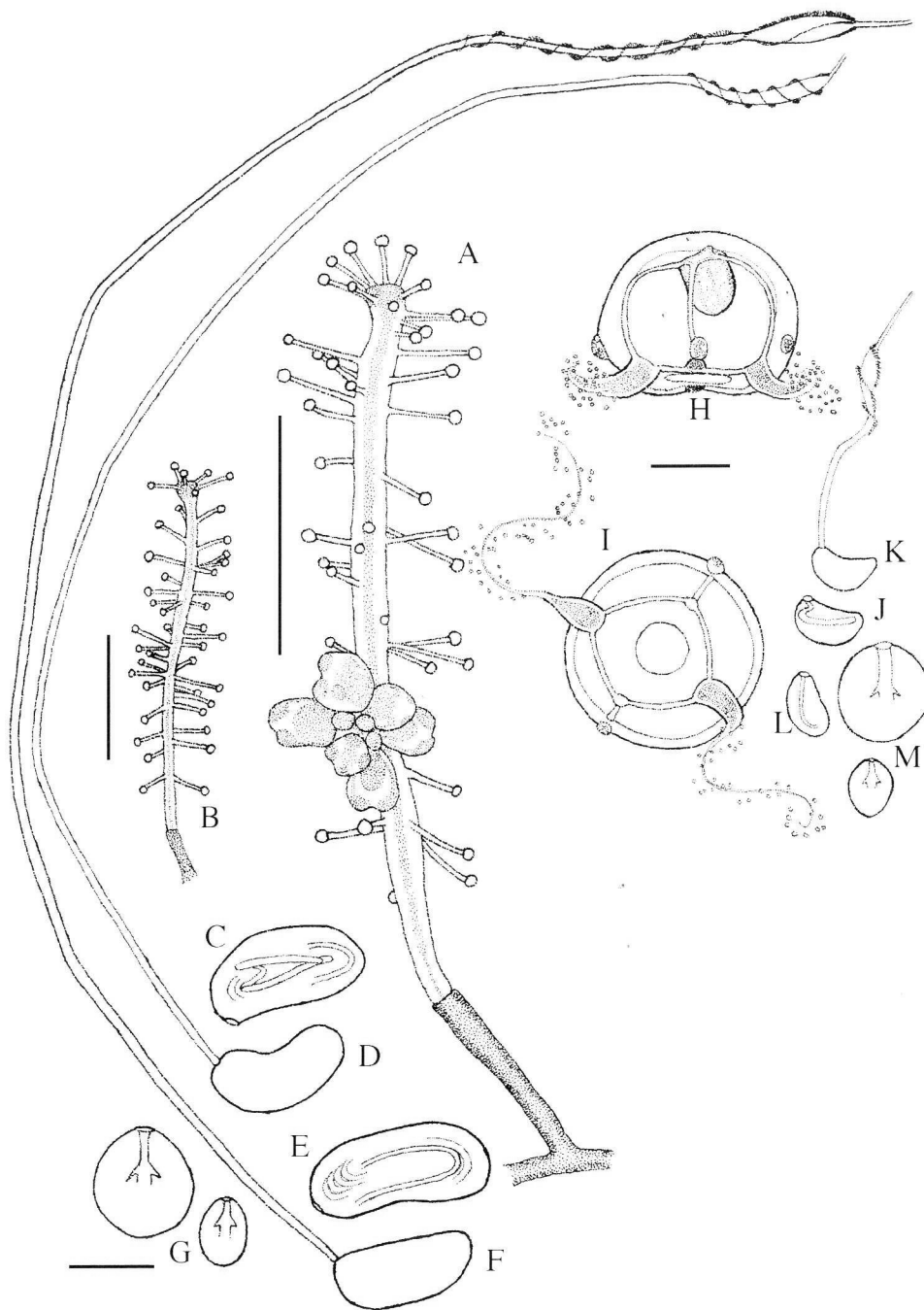


FIG. 4. – *Zanclea* sp. A: living hydranth with medusa buds; B: living hydranth; C: hydroid, undischarged small macrobasic eurytele; D: the same, discharged; E: hydroid, undischarged large macrobasic eurytele; F: the same, discharged; G: hydroid, undischarged stenoteles of two sizes; H: newly released medusa in side view; I: newly released medusa from below; J: medusa, undischarged macrobasic eurytele; K: the same, discharged; L: medusa, microbasic euryteles (?); M: medusa undischarged stenoteles of two sizes. Bar scales: A, B: 1 mm; H, I: 0.2 mm; all nematocysts: 0.01 mm.

Species-specific cell adhesion on the extracellular matrix of *Zanclea sessilis* and *Zanclea* sp.

Following the technique described by Schmid *et al.* (1992), implants of tissues of *Zanclea sessilis*

were attempted on the mesogloea of the same species and on that of *Zanclea* sp., and the same procedure was used to test the tissues of *Zanclea* sp. against the mesogloea of both *Zanclea sessilis* and *Zanclea* sp. Cell adhesion occurred when the tissues

TABLE 1. – Main characters of the Mediterranean hydroids referred to *Zancklea*, excluding nematocysts (see Table 2).

	<i>Zancklea sessilis</i>	<i>Zancklea costata</i>	<i>Zancklea</i> sp.
Hydranth height	About 1 mm	2-3 mm	2-3 mm
Tentacle number	20-40	About 60	Above 50
Perisarc, thickness colour	Thin Whitish	Thick Brownish	Thick Brownish
Medusa buds, position	Below tentacled part of hydranth	Between tentacles in mid-low part of hydranth	Among tentacles in lower third of hydranth
Hydroid plasticity	Reduction or lack of tentacles in hydranths with medusa buds		High morphological plasticity, with stolonization and hydranth formation in area of medusa bud production
Substrate	On bryozoan (<i>Beania</i> sp.)	On <i>Cardium</i> sp. shell	On bryozoan sp.

were from the same “morphological” species, whereas rejection was observed when the tissues were from different “morphological” species, reinforcing the treatment of *Zancklea sessilis* as distinct from *Zancklea* sp.

DISCUSSION

The features allowing morphological distinction among the three *Zancklea* species recorded from the Mediterranean Sea are shown in Table 1, and Table 2 shows details of their cnidomes. Brinkmann-Voss (1970) has already reported that *Zancklea* hydroids living on bivalves maintained a constant difference

from those growing on bryozoans, even when kept under the same culture conditions for a long time. This is confirmed here and demonstrates that, in spite of a wide range of intraspecific variation, *Zancklea* species do not “merge” into each other, as suggested by Russell and Rees (1936), since the range of variation of a single colony does not cover the whole spectrum of morphological differentiation on which nominal species were based. Nematocyst type and structure, furthermore, is an unambiguous character which allows prompt identification and is to be considered as the main diagnostic feature for *Zancklea* species, at least in the hydroid stage. The medusa is more problematic because some characters seem variable with age and environmental con-

TABLE 2. – Nematocysts of the Mediterranean hydroids referred to *Zancklea*.

	<i>Zancklea sessilis</i>	<i>Zancklea costata</i>	<i>Zancklea</i> sp.
Type	Apotrichous macrobastic euryteles, stenoteles	Holotrichous macrobastic euryteles, microbastic euryteles (?) stenoteles	Apotrichous macrobastic euryteles of two types, stenoteles
Position			
macr. euryteles	In a circle between oral tentacles and in hydrorhiza, rare in hydranth body	Abundant in hydrorhiza, rare in hydranth body	Present in hydrorhiza and in hydranth body
stenoteles	In tantacle capitula	In tantacle capitula	In tantacle capitula
micr. euryteles (?)	Absent	Rare in tantacle capitula	Absent
Shaft of macr. euryteles	Coiled in a horseshoe shape	Spiral-shaped	Coiled along the long axis of capsule
Spines on shaft of macr. euryteles	On one fifth of shaft	Along the whole shaft	a) On one fifth of shaft b) On one tenth of shaft

ditions, and cnidome is more uniform between species than in the hydroid. A constant feature of the medusa of *Zanclea sessilis*, however, was the presence of enlargements in the radial canals, from the release to maturity. The medusa of *Zanclea* sp. did not have such a feature on release. Further, the medusa of *Z. sessilis* reacted differently from that of *Z. sp.* to identical culture conditions, and this reinforces treating them as different species. Even though colonies were kept under the same controlled conditions, *Zanclea sessilis* produced medusae in different periods from *Z. sp.*, this suggesting the two species as having differently tuned circannual clocks regulating medusa production (see, for instance, Brock, 1975). This displacement in the timing of medusa production could also account for reproductive isolation leading to sympatric speciation.

Zanclea hydroids live both on hard and soft bottoms, and have colonised a wide range of microhabitats, linked to a sharp tendency towards symbiotic relationships. Species separation due to hydroid host choice, however, should be almost impossible because the medusae could easily interbreed if present in the plankton in the same period. It might be predicted that species linked to hard bottoms would have shorter-lived medusae (since such bottoms are limited to coastal areas), whereas those living on mollusc shells inhabiting soft bottoms might have longer-lived medusae, since such environments are widespread and the risk of not finding a proper substratum by over-dispersed planulae (due to medusa over-dispersal) is low.

It is highly probable that the medusae reported by both Berhaut (1969) and Goy (1972) as having two tentacles and swollen radial canals at maturity are *Zanclea sessilis*, the species the hydroid of which lives on bryozoans and whose medusae have paedomorphic features. *Zanclea* medusae with four tentacles and straight radial canals would be *Zanclea costata* (the hydroid of which grows on bivalves). The hydroid of this species is very similar, in gross morphology, to that of our *Zanclea* sp. (growing on bryozoans), but nematocyst differences indicate that the two are to be kept distinct. Cnidome has rarely been considered in the original descriptions of *Zanclea* hydroids and, further, its features tend to become unclear in preserved material (especially when kept in spirit), so that type specimens are unreliable in identification. The cnidomes of the medusa stages are more uniform than those of hydroids. This is so although some differences can be detected in the exumbrellar armature of newly released medu-

sae, a feature which, however, disappears a few days after liberation (see, for instance, the presence of supposed microbasic euryteles in *Zanclea* sp.). Medusae are more difficult to keep in the laboratory than hydroids, but rearing medusae derived from a single colony (to assess intraspecific variation) still seems the only method to study the actual range of variation of medusae deriving from hydroids identified on cnidome. Species-specificity of cell adhesion to extracellular matrix (Schmid *et al.*, 1992) is a useful taxonomic tool and reinforced the value of the morphological differences between *Zanclea sessilis* and *Zanclea* sp.

The merging of all *Zanclea* nominal species into *Z. costata* by Russell (1953) greatly influenced ideas concerning *Zanclea* taxonomy. The present findings, however, prove that the conclusions of Russell (1953), stemming from Russell and Rees (1936), were incorrect, supporting the validity of the positions of Hastings (1930), Picard (1965), Millard and Bouillon (1973). *Zanclea* hydroids are symbiotic with a vast array of animals. Possibly specialization towards different hosts led to speciation with a greater differentiation of the hydroid (due to adaptation to different conditions determined by host choice) than of the medusa, the planktonic habitat of this stage being somehow identical for the medusae of all species. As remarked above, however, the medusae reached maturity at different degrees of growth (paedomorphosis) and were released at different times of year, this allowing sympatric speciation via separation of reproductive activity. Specialization to grow exclusively on serpuloid opercula, furthermore, probably led to *Teissiera*, a zancleoid genus differing from *Zanclea* in the hydroid stage but not in the medusa, the only difference being the presence of ocelli in *Teissiera*, absent from *Zanclea* (see Bouillon, 1974).

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REFERENCES

- Alder, J. – 1857. A Catalogue of the zoophytes of Northumberland and Durham. *Trans. Tyneside Nat. Field Club* 3: 93-162.
- Berhaut, J. – 1969. Etude qualitative, quantitative et écologique des Hydroméduses du Golfe de Marseille. *Tethys* 1(3): 667-708.
- Boero, F. and J. Bouillon. – 1993. Zoogeography and life cycle patterns of Mediterranean hydromedusae (Cnidaria). *Biol. J. Linn. Soc.* 48: 239-266.
- Boero, F., J. Bouillon and N. Gravier-Bonnet. – 1995. The life cycle of *Pteroclava kremphi* (Cnidaria, Hydrozoa, Cladocorynidae), with some notes on *Asyncoryne philippina* (Asyncorynidae). *Sci. Mar.* 59(1): 65-76.
- Bouillon, J. – 1974. Description de *Teissiera milleporoides*, nouveau genre et nouvelle espèce de Zancleidae des Seychelles (Hydrozoaires; Athécates-Anthomédues), avec une révision des Hydroides "Pteronematoidea". *Cah. Biol. Mar.* 15: 113-154.
- Bouillon, J. – 1978. Hydroméduses de la mer de Bismarck (Papouasie, Nouvelle-Guinée). I. - Anthomédues Capitata (Hydrozoa-Cnidaria). *Cah. Biol. Mar.* 19: 249-297.
- Bouillon, J. – 1985. Essai de classification des hydropolypes-hydroméduses (Hydrozoa-Cnidaria). *Indo-Malayan Zool.* 1: 29-243.
- Brinkmann-Voss, A. – 1970. Anthomédues/Athécates (Hydrozoa, Cnidaria) of the Mediterranean. Part I Capitata. *Fauna e Flora del Golfo di Napoli* 39: 1-96.
- Brock, M.A. – 1975. Circannual rhythms - III Rhythmicity in the longevity of the hydranths of the marine cnidarian, *Campanularia flexuosa*. *Comp. Biochem. Physiol.* 51 A: 391-398.
- Browne, E.T. – 1916. Medusae from the Indian ocean. *Trans. Linn. Soc. Lond. (Zool.)* 17: 169-210.
- Brückner, E. – 1914. Beitrag zur Kenntnis von *Perigonimus cidaritis* Weismann und *Gemmaria implexa* var. *neapolitana* Hargitt. *Z. Wiss. Zool., Leipzig* 111: 445-505.
- Calder, D. – 1988. Shallow-water hydroids of Bermuda: the Athecatae. *Roy. Ont. Mus., Life Sci. Contr.* 148: 1-107.
- Calder, D. – 1992. Case 2806. *Zanclea costata* Gegenbaur, 1856 (Cnidaria, Hydrozoa): proposed conservation of both generic and specific names. *Bull. Zool. Nomenclature* 49: 184-186.
- Gosse, P.H. – 1853. *A naturalist's rambles on the Devonshire coast*. John van Voorst. London.
- Goy, J. – 1972. Les hydroméduses de la mer Ligure. *Bull. Mus. nat. Hist. Nat. 3^e sér.* 83, Zool. 62: 965-1009.
- Hastings, A.B. – 1930. On the Association of a Gymnoblasic Hydroid (*Zanclea protecta*, sp. n.) with various Cheilostomatous Polyzoa from the Tropical E. Pacific. *Ann. Mag. Nat. Hist. ser.* 10, 5: 552-560.
- Hincks, T. – 1868. *A history of British Hydroid Zoophytes*. John van Voorst. London.
- Hirohito. – 1988. *The hydroids of Sagami Bay*. Biological Laboratory Imperial Household, Tokyo.
- International Commission On Zoological Nomenclature. – 1994. Opinion 1752. *Zanclea costata* Gegenbaur, 1856 (Cnidaria, Hydrozoa): generic and specific names conserved. *Bull. Zool. Nomenclature* 51 (1): 54-55.
- Kramp, P.L. – 1961. Synopsis of the medusae of the world. *J. Mar. Biol. Ass. U. K.* 40: 1-469.
- Mammen, T. – 1963. On a collection of hydroids from South India. *J. Mar. Biol. Ass. India* 5: 27-61.
- McCrary, J. – 1859. Gymnophthalmata of Charleston Harbor. *Proc. Elliott Soc. Nat. Hist.* 1: 103-221.
- Millard, N.A.H. and J. Bouillon. – 1973. Hydroids from the Seychelles (Coelenterata). *Ann. Mus. Roy. Afr. Centr. (Zool.)* 206: 1-106.
- Petersen, K. – 1990. Evolution and taxonomy in capitate hydroids and medusae. *Zool. J. Linn. Soc.* 100: 101-231.
- Picard, J. – 1965. *Recherches qualitatives sur les biocénoses marines des substrats meubles dragables de la région marseillaise*. Ph. D. thesis, univ. Aix-Marseille.
- Rees, W.J. and E. Roa. – 1966. Asexual reproduction in the medusa *Zanclea implexa* (Alder). *Vidensk. Medd. fra Dansk naturh. Foren.* 129: 39-41.
- Russell, F.S. – 1953. *The medusae of the British Isles. Anthomédues, Leptomédues, Limnomédues, Trachymédues and Narcomédues*. Cambridge Univ. Press, Cambridge.
- Russell, F.S. and W.J. Rees. – 1936. On rearing the hydroid *Zanclea implexa* (Alder) and its medusa *Zanclea gemmosa* McCrary, with a review of the genus *Zanclea*. *Journ. Mar. Biol. Assoc. U. K.* 21: 107-128.
- Schmid, V., P. Schuchert, S. Piraino and F. Boero. – 1992. The mesogloea (extracellular matrix) of hydrozoans can be species-specific for cell attachment and cell migration: a new tool for taxonomists? In: J. Bouillon, F. Boero, F. Cicogna, J.M. Gili and R.G. Hughes (eds): *Aspects of Hydrozoan biology*. *Sci. Mar.* 56 (2-3): 131-136.
- Uchida, T. and Y. Sugiura. – 1976. On a hydromedusa, *Zanclea prolifera* n. sp., of which the medusa gives rise to medusa-buds. *Proc. Japan. Acad.* 52 (3): 141-144.
- Vannucci, M. – 1960. On the intraspecific variation and biology of *Merga tergestina* (Anthomédues, Pandeidae). *Pubbl. Staz. Zool. Napoli* 31: 393-420.
- Weill, R. – 1934. Contribution à l'étude des Cnidaires et de leurs nématocystes. *Trav. Stat. Zool. Wimereux* 10-11: 1-701.